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Systematics, taxonomy, and distribution of species of *Myriogenospora* G.F. Atk. (Clavicipitaceae, Hypocreales, Ascomycota)

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Abstract

Based on new specimens of *Myriogenospora* spp. from Costa Rica and Panama, we present morphological analyses, systematic conclusions, additions to host ranges, and geographical distribution data for the two species currently classified in this genus. *Myriogenospora atramentosa* (Berk. & M.A. Curtis) Diehl differs from *Myriogenospora linearis* (Rehm) J.F. White & Glenn in the ascus and part-spore morphology, a different position in the molecular phylogeny, and the host range. We conclude that the two species are not congeneric and propose that *M. linearis* should be called *Balansia linearis* (Rehm) Diehl.

Keywords

Balansia, Clavicipitaceae, Costa Rica, grass epibionts, Panama, phylogeny, Poaceae.

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Introduction

The wide host range and diverse host interactions of clavicipitaceous fungi have led to a series of studies on the ecology (Saikkonen et al. 2006), evolution (Kepler et al. 2012b), toxicology (Bacon et al. 1975; Kallenbach 2015), and biotechnological application (Kusari et al. 2014) of species of Clavicipitaceae (Hypocreales, Ascomycota). To address these topics, knowledge on the morphology, systematics, taxonomy, host range, and geographical distribution is important. Several studies have paid special attention to plant-infecting species of Clavicipitaceae including those classified in the tribe Balansieae or the *Ephelis* clade (Kuldau et al. 1997). These species can increase plant resistance against herbivory (Clay et al. 1985, 1989) and drought (Ren and Clay 2009), and some of their metabolites could have medicinal and agricultural applications (Tan and Zou 2001). However, few studies have contributed to our knowledge on the distribution and systematics of balansioid fungi in recent years. Therefore, many species concepts rely only on morphological observations with DNA sequence data being incomplete or entirely missing.

The genus *Myriogenospora* G.F. Atk. was established by Atkinson (1894) and includes *M. atramentosa* (Berk. & M.A. Curtis) Diehl (type species, syn. *M. paspali* G.F. Atk.) and *M. linearis* (Rehm) J.F. White & Glenn according to the most recent taxonomic revision by White and Glenn (1994). *Myriogenospora* spp. are characterized by perithecia arranged in lines embedded in linear stromata parallel to and mostly surrounded by grass leaf blades

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(Poaceae). The asci are fusiform and, as the genus name indicates, they include numerous part-spores. These part-spores are small, fusoid, and result from ascospore fragmentation and bipolar growth with secondary spore production (White and Glenn 1994).

Using recently collected samples from both species of *Myriogenospora,* we reassess the geographical distribution, host range, morphological descriptions, and systematic relationships of *M. atramentosa* and *M. linearis.*

Methods

During field sampling of plant-parasitic microfungi in southern Central America, we collected several specimens of *Myriogenospora* spp. in Costa Rica and Panama between 1992 and 2015. Collection sites with ecological details are mentioned together with the records below. Dried specimens were deposited in the following herbaria: specimens collected in Costa Rica were deposited in the Herbario de la Universidad de Costa Rica (USJ), and specimens from Panama in the Herbario de la Universidad de Panama (PMA) and the Herbario de la Universidad de Chiriqui (UCH). All the specimens were also deposited in the Botanische Staatssammlung, München (M), Germany.

We examined the morphology of *Myriogenospora* spp. using dry material in 10% KOH with or without aniline blue aqueous solution. Using a freezing microtome Leica (CM 1510-1), we obtained microscopic, about 30 µm thick sections to image the stroma morphology. Imaging and measurements were done using a camera Nikon DS-Fi2 adapted to the microscope and operated by the imaging software NIS-Elements D 2.2. The measurements indicate the mean value ± the standard deviation of *n* measurements ($n \geq 20$) and extreme values in parentheses. Line drawings were traced using a drawing tube and edited with Photoshop CS5 (Adobe, San Jose, California).

DNA extraction and PCR protocols followed the procedure described by Mardones et al. (2017). Three partial nuclear gene regions (two ribosomal loci and one protein-coding gene) were amplified and sequenced: a fragment of the large subunit nuclear ribosomal DNA (nrLSU) with primers NL1 and NL4 (O'Donnell 1993), the complete internal transcribed spacer region of ribosomal DNA (ITS1-5.8S-ITS2) with primers ITS5 and ITS4 (White et al. 1990), and a fragment of the translation elongation factor 1 (TEF1*)* with primers EF1-983f (Carbone and Kohn 1999) and EF1-2218r (Rehner and Buckley 2005).

For phylogenetic analyses of *Myriogenospora* spp. and other Clavicipitaceae, we compiled a three-locus concatenated alignment (nrLSU, ITS, TEF1) including 33 species. These analyses were rooted using *Tolypocladium capitatum* (Holmsk.) C.A. Quandt, Kepler & Spatafora and *T. japonicum* (Lloyd) CA Quandt, Kepler & Spatafora (Ophiocordycipitaceae) as outgroups. The taxa of Clavicipitaceae used in the analyses as well as the newly generated sequences deposited in GenBank are listed in Table 1 together with their locality, host plant, voucher numbers, and GenBank accession numbers. The alignments were deposited in TreeBASE (http://www.treebase.org/) under accession number 24171.

Phylogenetic analyses were conducted applying maximum likelihood (ML) and Bayesian methods and followed the procedures outlined by Mardones et al. (2017). Data were partitioned by gene and by codon position in the case of the protein-coding sequences. The HKY + G model was applied to ITS, GTR + I + G model to nrLSU, and TIM + I + G model to TEF1. Bayesian posterior probabilities (BPP) ≥0.95 and Bootstrap values (BS) ≥70 were considered to be significant.

Results

***Balansia linearis* (Rehm) Diehl**, Agric. Monogr. No. 4: 47 (1950)
Figures 1, 2, 3A

Material examined. Costa Rica • Cartago Province, Cerro de la Muerte, Cerro de la Asunción, Pan-American Highway km 89, near the entrance of the Tapantí National Park; alt. about 3100 m a.s.l.; 10 Jan. 2015; M. Piepenbring, O. Cáceres, M. Eichenlaub, M. Mardones leg.; on leaves of *Chusquea subtessellata* Hitchc. (det. M. Piepenbring) (MP 5242; M 141351; USJ109414).

Identification. Infected shoots of the host plant without flowers and with all leaves presenting stromata. Stromata wrapped in host leaf blades except for a linear exposed part containing perithecia, epibiotic, one to several centimeters long, hyaline except for a black outer surface. Leaf blades held in rolled position (supervolute ptyxis) by a plectenchyma consisting of fungal cells. Perithecia immersed, arranged in 1–2 rows, pyriform or bottle-shaped, (475–)505–590(–625) × (225–)265–375(–405) µm. Ostioles appear as warts on the black outer stroma surface. Asci cylindrical, unitunicate, containing numerous part-spores, (150–)170–250(–280) × (5.5–)6.5–9.5(–11) µm (difficult to measure because the asci intermingle and easily break), with a truncate, light refractive body perforated by a central pore at the tip of each ascus. Part-spores cylindrical, containing guttules, (17–)21–27(–28) × 1.0–1.5 µm, hyaline, smooth. No part-spore initials resulting from ascospores fragmentation followed by reinitiated bipolar growth were observed.

Synonyms. *Ophiodothis linearis* Rehm. *Linearistroma lineare* (Rehm) Höhn. *Myriogenospora linearis* (Rehm) J.F. White & Glenn.

Type. Brazil, Campo Bello, on *Chusquea* sp., 1894, E. Ule 2105 (type, n.v., not in BPI).

For heterotypic synonyms see White and Glenn (1994).

Known distribution. Until now, *Balansia linearis* (*M. linearis*) is only known from Brazil (Pazschke 1896). Here, we report this species for the first time for Costa Rica and for the first time outside of Brazil (Fig. 3A).

Table 1. Specimen data of plant-infecting species of the family Clavicipitaceae included in the phylogenetic analyses. Accession numbers written in **bold** refer to sequences generated during the present study. [1] More exact location data are not available.

Species	Locality	Host Plant	Voucher	GenBank accession numbers			Reference(s)
				ITS	28S rDNA	TEF1	
Balansia brunnans E.A. Lewis & J.F. White	Mexico	*Panicum laxiflorum* Lam.	ATCC MYA-2105		AY327046		Lewis et al. (2002)
Balansia claviceps Speg.	India	*Cyrtococcum oxyphyllum* (Steud.) Stapf	CBS 501.70	MH859816	MH871588		Vu et al. (2019)
Balansia cyperi Edgerton	USA	*Cyperus virens* Michx.	B1075		U68118		Kuldau et al. (1997)
Balansia discoidea Henn.	Costa Rica	*Panicum pilosum* Sw.	MP 5239b		MK660205	MN104684	
Balansia epichloë (Weese) Diehl	Americas[1]	Poaceae	AEG 96-15a	JN049848		EF468743	Sung et al. (2007); Kepler et al. (2012a)
Balansia epichloë (Weese) Diehl	Americas[1]	*Sporobolus indicus* (L.) R.Br.	B113		U68121		Kuldau et al. (1997)
Balansia henningsiana (Möller) Diehl	USA	*Panicum* sp.	AEG96-27a	JN049815	AY489715	AY489610	Castlebury et al. (2004); Kepler et al. (2012a)
Balansia hypoxylon (Peck) G.F. Atk.	USA	*Danthonia spicata* (L.) Roem. & Schult.	B112		U68114		Kuldau et al. (1997)
Balansia linearis (Rehm) Diehl (*Myriogenospora linearis* (Rehm) J.F. White & Glenn)	Costa Rica	*Chusquea subtessellata* Hitchc.	MP 5242	**MK660199**	MK660212		
Balansia nigricans (Speg.) J.F. White, T.E. Drake & T.I. Martin	USA	*Axonopus furcatus* (Flüggé) Hitchc.	B252		U68119		Kuldau et al. (1997)
Balansia obtecta Diehl	Americas[1]	*Cenchrus echinatus* L.	B249	JFZS01000644	JFZS01000644	KP689549	Schardl et al. (2014)
Balansia pilulaeformis (Berk. & M.A. Curtis) Diehl	USA	*Chasmanthium laxum* (L.) H.O.Yates	ATCC 90722		U68122		Kuldau et al. (1997)
Balansia sp.	Mexico	*Bothriochloa pertusa* (L.) A. Camus	MP 1934		MK660204		
Balansia strangulans (Mont.) Diehl	Americas[1]	*Panicum aciculare* Desv.	B493		U68124		Kuldau et al. (1997)
Balansia texensis (Diehl) P.V. Reddy, Clay & J.F. White	Americas[1]	*Nassella leucotricha* (Trin. & Rupr.) R.W.Pohl	B6155			KP689547	Schardl et al. (2014)
Claviceps africana Freder., Mantle & De Milliano	USA	*Sorghum* sp.	USDA BPI 806256		AF245294		Sullivan et al. (2001)
Claviceps fusiformis Loveless	Unknown	Unknown	ATCC 26019		U17402	DQ522320	Rehner and Samuels (1995); Spatafora et al. (2007)
Claviceps paspali F. Stevens & J.G. Hall	Italy	*Paspalum distichum* L.	ATCC 13892		U68127	DQ522321	Kuldau et al. (1997); Spatafora et al. (2007)
Claviceps ranunculoides Möller	Costa Rica	*Setaria* sp.	Unknown		AF245295		Sullivan et al. (2001)
Ephelis japonica Henn.	Japan	Unknown	NIAES 6584	AB114631			Yokoyama et al. (2006)
Epichloë amarillans J.F. White	USA	*Agrostis hyemalis* (Walter) Britton, Stern & Poggenb.	E 57	L07142		KP689562	Tsai et al. (1994)
Epichloë amarillans J.F. White	USA	*Sphenopholis obtusata* (Michx.) Scribn.			U57680		Suh et al. (1998)
Epichloë baconii J.F. White	Europe[1]	*Calamagrostis villosa* (Chaix) J.F. Gmel.	ATCC 200745	JFGY01000975	JFGY01000975	KP689561	Schardl et al. (2014)

Table 1. *Continued.*

Species	Locality	Host Plant	Voucher	GenBank accession numbers			Reference(s)
				ITS	28S rDNA	TEF1	
Epichloë brachyelytri Schardl & Leuchtm.	North America[1]	*Brachyelytrum erectum* (Schreb.) P.Beauv.	E4804			KP689564	Schardl et al. (2014)
Epichloë bromicola Leuchtm. & Schardl	Eurasia[1]	*Bromus tomentellus* Boiss.	AL0434			KP689558	Schardl et al. (2014)
Epichloë coenophiala (Morgan-Jones & W. Gams) C.W. Bacon & Schardl	Europe[1]	*Festuca arundinacea* Schreb.	ATCC 90664 (E19)		U68115	KP689556	Kuldau et al. (1997); Schardl et al. (2013)
Epichloë elymi Schardl & Leuchtm.	USA	*Elymus villosus* Muhl. ex Willd.	ATCC 201555		AY986924		Chaverri et al. (2005)
Epichloë festucae Leuchtm., Schardl & M.R. Siegel	Unknown	*Festuca rubra* L.	E32		U68116		Kuldau et al. (1997)
Epichloë glyceriae Schardl & Leuchtm.	USA	*Glyceria striata* (Lam.) Hitchc.	ATCC 200747	L07136	AFRG01001328	KP689560	Kuldau et al. (1997); Schardl et al. (2013)
Epichloë sylvatica Leuchtm. & Schardl	Germany	*Brachypodium sylvaticum* (Huds.) P. Beauv.	HLW 2038	MK660198	MK660206	MN104680	present study
Epichloë typhina (Pers.) Brockm.	New Zealand	*Festuca rubra* L.	ATCC 56429	JN049832	U17396	AF543777	Rehner and Samuels (1995); Currie et al. (2003); Kepler et al. (2012a)
Myriogenospora atramentosa (Berk. & M.A. Curtis) Diehl	Costa Rica	*Homolepis aturensis* (Kunth) Chase	MP 528	MK660203	MK660211		Present study
Myriogenospora atramentosa (Berk. & M.A. Curtis) Diehl	Panama	*Axonopus compressus* (Sw.) P. Beauv.	MP 5114	MK660202	MK660210	**MN104685**	Present study
Myriogenospora atramentosa (Berk. & M.A. Curtis) Diehl	Panama	*Homolepis aturensis* (Kunth) Chase	MP 5113	MK660201	MK660209		Present study
Myriogenospora atramentosa (Berk. & M.A. Curtis) Diehl	Panama	*Paspalum conjugatum* P.J. Bergius	MP 4953		MK660207		Present study
Myriogenospora atramentosa (Berk. & M.A. Curtis) Diehl	USA	*Andropogon virginicus* L.	AEG 96-32	JN049835	AY489733		Castlebury et al. (2004); Kepler et al. (2012a)
Nigrocornus scleroticus (Pat.) Ryley	Benin	*Andropogon gayanus* Kunth	LB2015_09-24/1		MK660213	MN104683	present study
Nigrocornus scleroticus (Pat.) Ryley	Benin	*Andropogon gayanus* Kunth	LB2015_09-17/2		MK660214	MN104681	present study
Nigrocornus scleroticus (Pat.) Ryley	Benin	*Andropogon schirensis* Hochst.	LB2015_09-18/3		MK660215	MN104682	present study
Nigrocornus scleroticus (Pat.) Ryley	India	*Cymbopogon citratus* (DC.) Stapf	ATCC 18154		U68123		Kuldau et al. (1997)
Nigrocornus scleroticus (Pat.) Ryley	India	*Cymbopogon citratus* (DC.) Stapf	CBS 365.67		MH870695		Vu et al. (2019)
Nigrocornus scleroticus (Pat.) Ryley	India	Unknown	ATCC 16582		U47821		Spatafora and Blackwell (1993)
Parepichloë cinerea (Berk. & Broome) J.F. White & P.V. Reddy	Nepal	*Sporobolus* sp.	Ne-01	AB065425			Tanaka et al. (2002)
Tolypocladium capitatum (Holmsk.) C.A. Quandt, Kepler & Spatafora	Japan	*Elaphomyces* sp.	NBRC 100997	JN943313	JN941401	AB968597	Schoch et al. (2012); Ban et al. (2015)
Tolypocladium japonicum (Lloyd) C.A. Quandt, Kepler & Spatafora	Unknown	*Elaphomyces* sp.	OSC 110991	JN049824	DQ518761	DQ522330	Spatafora et al. (2007); Kepler et al. (2012a)

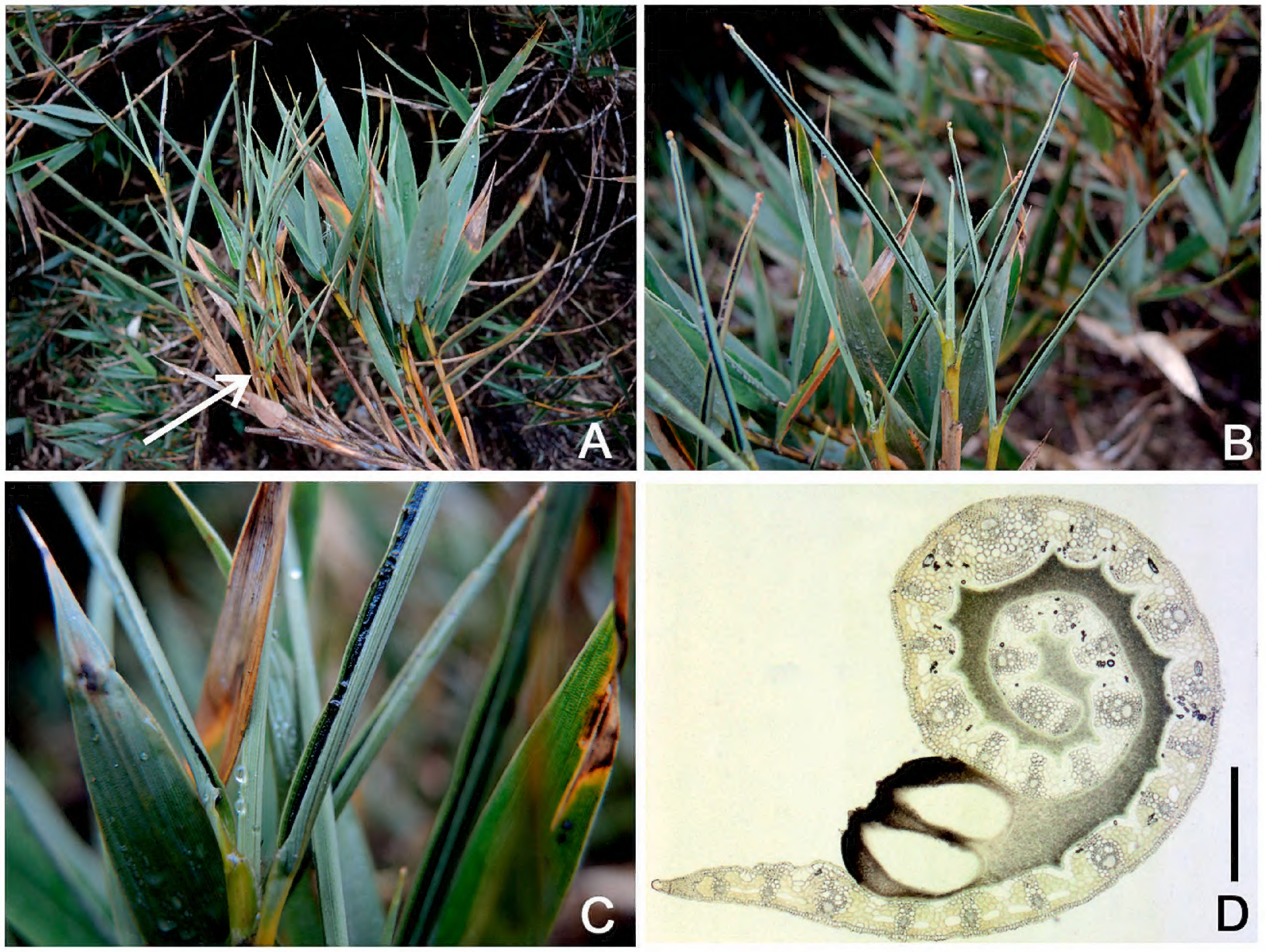

Figure 1. *Balansia linearis* (*Myriogenospora linearis*) on leaves of *Chusquea subtessellata* (MP 5242). **A–C.** Fresh specimen in the field. **A.** Infected shoot (arrow) and healthy shoot (right). **B.** Infected shoots. **C.** One linear stroma with ostioles of perithecia evident as warts. **D.** Transverse section of a leaf blade held in a rolled position by the fungal stroma including two perithecia below the black surface of the stroma as seen by light microscopy. Scale bar = 500 µm.

Host plants. Until now, *Balansia linearis* (*M. linearis*) is known from *Chusquea* sp., *Olyra micrantha* Kunth, *Pariana* sp. (Möller 1901; White and Glenn 1994), and *Merostachys speciosa* Spreng. (Möller 1901, cited as "*Microstachys speciosa* Spr.", see explanation below) all classified in Bambusoideae (Poaceae). Here, we report *B. linearis* (*M. linearis*) on *Chusquea subtessellata* as a new host plant species.

Möller (1901) reported *Ophiodothis raphidospora* Rehm (syn. of *Myriogenospora linearis* according to White and Glenn, 1994) on *Microstachys speciosa* Spr. for Brazil. The name of the host species is questionable as the genus *Microstachys* A. Juss. belongs to Euphorbiaceae and the name *Microstachys speciosa* is not validly published (see http://www.ipni.org). Due to the similar spelling of the name, the identical author, and the classification in Bambusoideae (Poaceae), we assume that Möller (1901) wanted to cite *Merostachys speciosa* Spreng.

Taxonomy. According to the most recent study on species of *Myriogenospora* presented by White and Glenn (1994), the fungus collected on *Chusquea subtessellata* in Costa Rica should be cited as *M. linearis* (Rehm) J.F. White & Glenn. We consider an older name, *Balansia linearis* (Rehm) Diehl, to be more convenient based on molecular sequence data, microscopical characteristics, and the host relationship (for details see below).

***Myriogenospora atramentosa* (Berk. & M.A. Curtis) Diehl**, Agric. Monogr. No. 4: 59 (1950)
Figures 3B, 4, 5

Material examined. Costa Rica • Limón Province, Valle de Talamanca, 26 Oct. 1992; M. Piepenbring leg., MP 528 (M 141354; USJ109407).

Panama • Chiriquí Province, Dolega, Los Algarrobos, path close to house of S. Cáceres; 08°29′36″ N, 082° 25′31″ W; alt. about 150 m a.s.l.; 8 Mar. 2010; M. Piepenbring, T. Hofmann leg.; MP 4953 (M 141355; PMA; UCH). • Chiriquí Province, border of road to Chiriquí Grande, before arriving at Fortuna, close to entrance of La Suiza; 08°39′24″ N, 082°12′37″ W; alt. about 1,150 m a.s.l.; 08 Mar. 2010; M. Piepenbring, O. Cáceres leg.; MP 4955 (M 141356; PMA; UCH). • Chiriquí Province, road to Chorogo; alt. about 400 m a.s.l.; 13 Jul. 2012; M. Piepenbring, D. Cáceres, A. Krohn, M. Rosas leg.; on leaves of *Homolepis aturensis* (Kunth) Chase (det. M. Piepenbring); MP 5113 (M 141357). • Chiriquí Province, road to Chorogo; alt. about 400 m a.s.l.; 13 July 2012; M. Piepenbring, D. Cáceres, A. Krohn, M. Rosas leg.; on

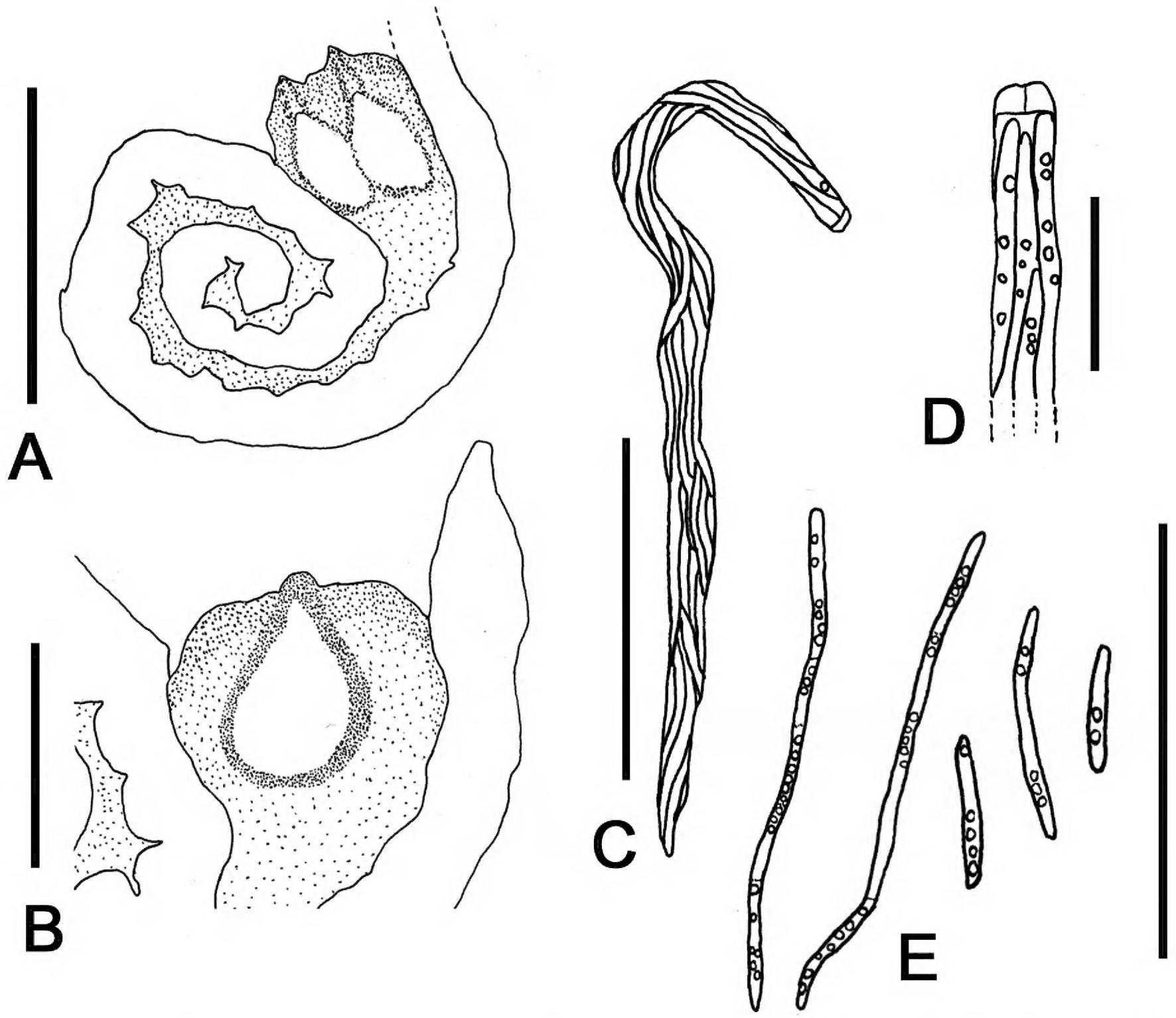

Figure 2. *Balansia linearis* (*Myriogenospora linearis*) on leaves of *Chusquea subtessellata* (MP 5242), as seen by light microscopy. **A.** Transverse section of a leaf blade with a fungal stroma (dots) including two perithecia. **B.** Part of a transverse section of an infected leaf with one perithecium. **C.** Ascus with ascospores. **D.** Ascus tip with a light refractive body. **E.** Ascospore fragments resulting from incomplete ascospore fragmentation (left) and cylindrical part-spores resulting from completed ascospore fragmentation. Scale bars: A = 1000 µm; B = 500 µm; C = 100 µm; D = 20 µm; E = 100 µm.

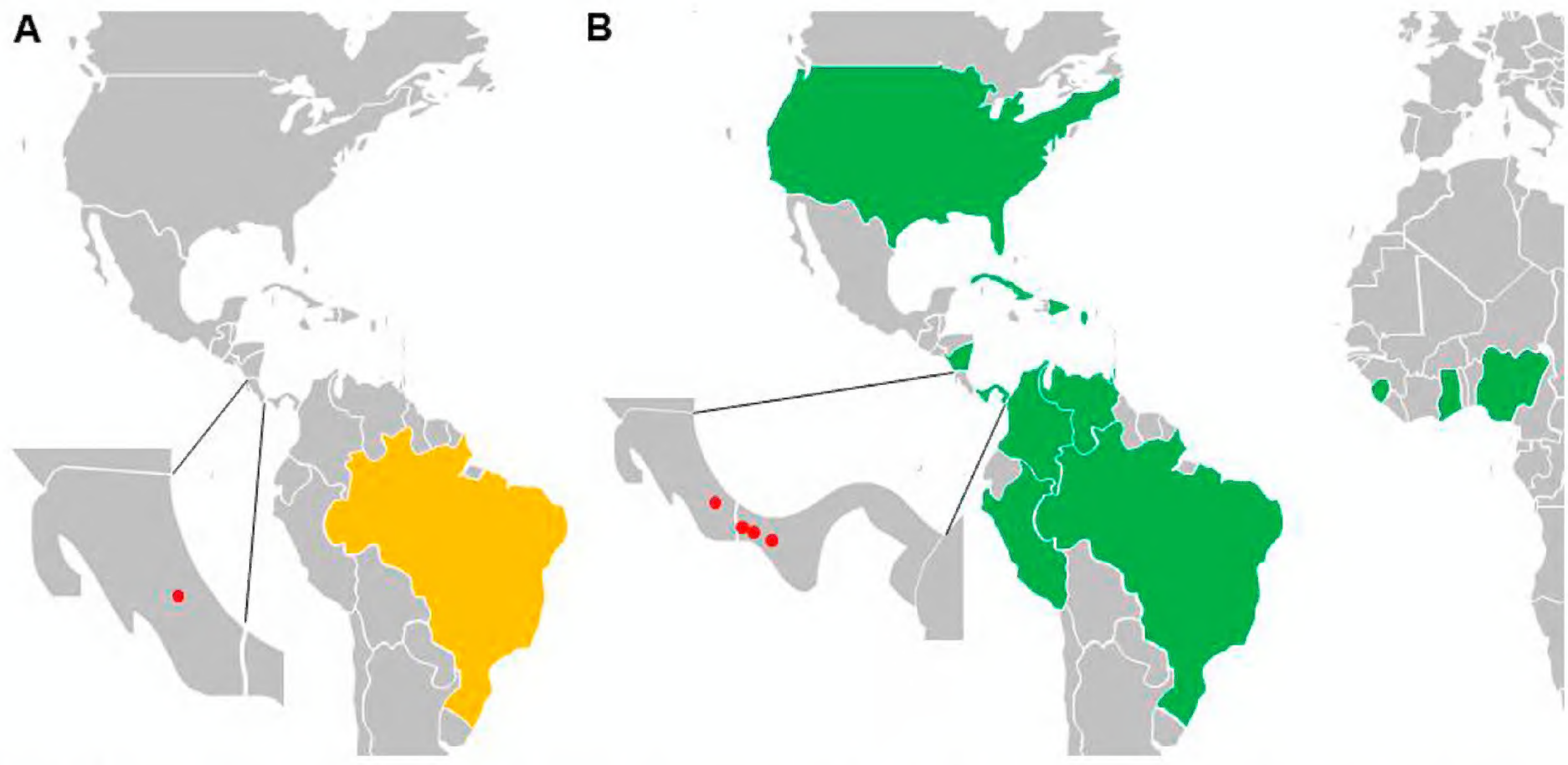

Figure 3. Maps showing known distribution and localities of new records and specimens. **A.** *Balansia linearis* (*Myriogenospora linearis*). **B.** *Myriogenospora atramentosa*. Localities of new records and specimens are indicated by red dots. The occurrence of these species in different countries according to literature is indicated by bright colors.

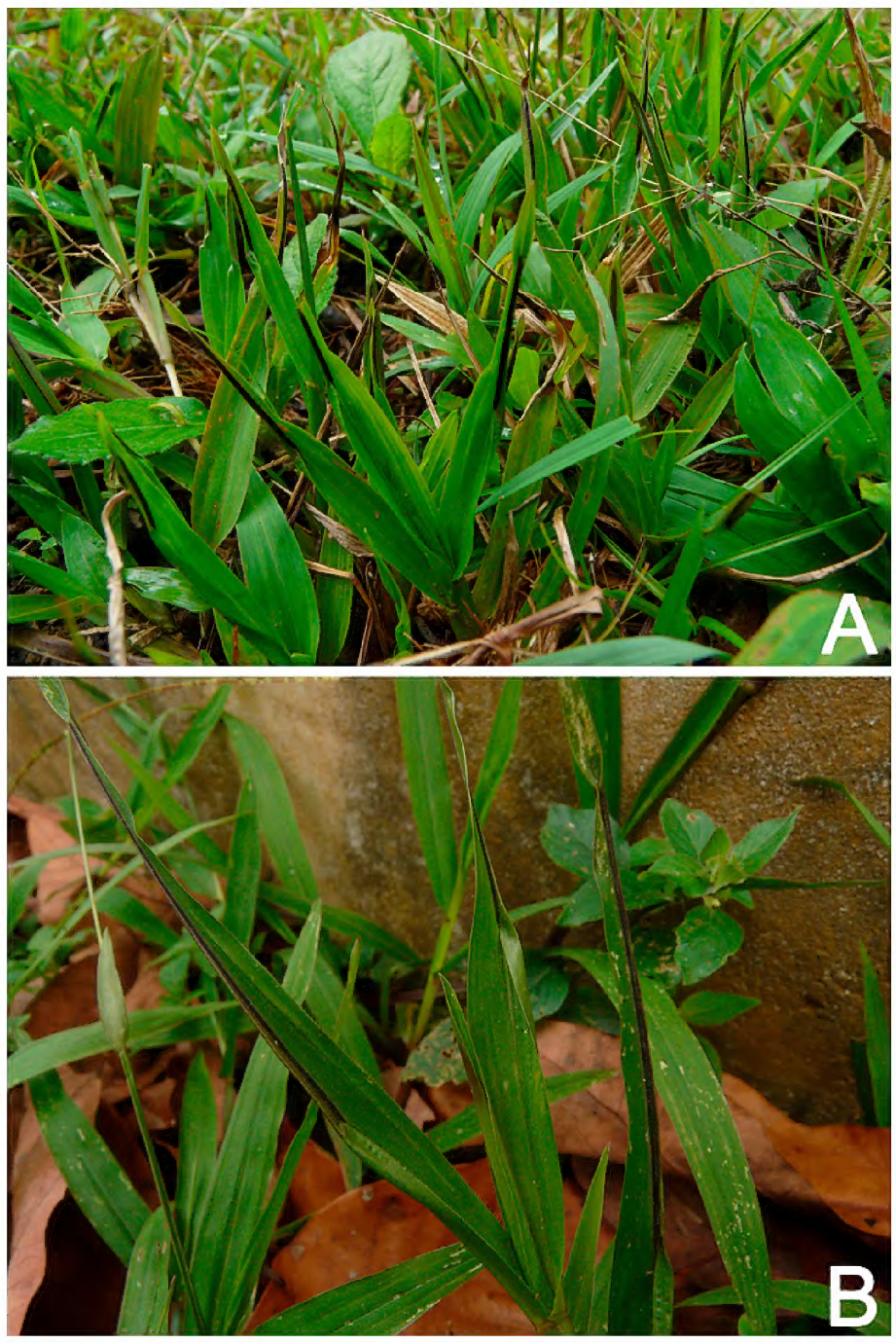

Figure 4. *Myriogenospora atramentosa* on leaves of *Paspalum conjugatum* in the field (MP 4953). **A.** Infected plants. **B.** An infected plant with black stromata wrapped in leaf blades.

leaves of *Axonopus compressus* (Sw.) P. Beauv. (det. M. Piepenbring); MP 5114 (M 141358).

Identification. Infected shoots of the host plants without flowers and with all leaves presenting stromata. Stromata wrapped in leaf blades except for a linear exposed part containing perithecia, epibiotic, one to several centimeters long, hyaline except for black outer surface. Leaf blades held together by a hyaline plectenchyma consisting of fungal mycelium in rolled or folded position (supervolute or conduplicate ptyxis). Perithecia immersed, arranged in one row, globose or subglobose, (225–)290–400(–465) × (235–)275–360(–440) µm. Ostioles appear as warts on the black outer stroma surface. Asci fusiform (cylindrical when young), unitunicate, containing numerous part-spores, (120–)135–255(–330) × (5–)8–16(–21) µm with dome-shaped ascus tips without light refractive bodies. Part-spore initials resulting from ascospore fragmentation ovoid to slightly fusiform, immediately growing at both tips and becoming mature part-spores, elongated fusoid, without septa, containing guttules, (20–)29–39(–45) × (0.5–)1.0–2.0 µm, hyaline, smooth.

Synonyms. *Hypocrea atramentosa* Berk. & M.A. Curtis. *Epichloë atramentosa* (Berk. & M.A. Curtis) Cooke. *Hypocrella atramentosa* (Berk. & M.A. Curtis) Sacc.

Type. Cuba, no date, on *Andropogon* sp., C. Wright 419 (holotype, K(M) 198287).

For heterotypic synonyms see White and Glenn (1994).

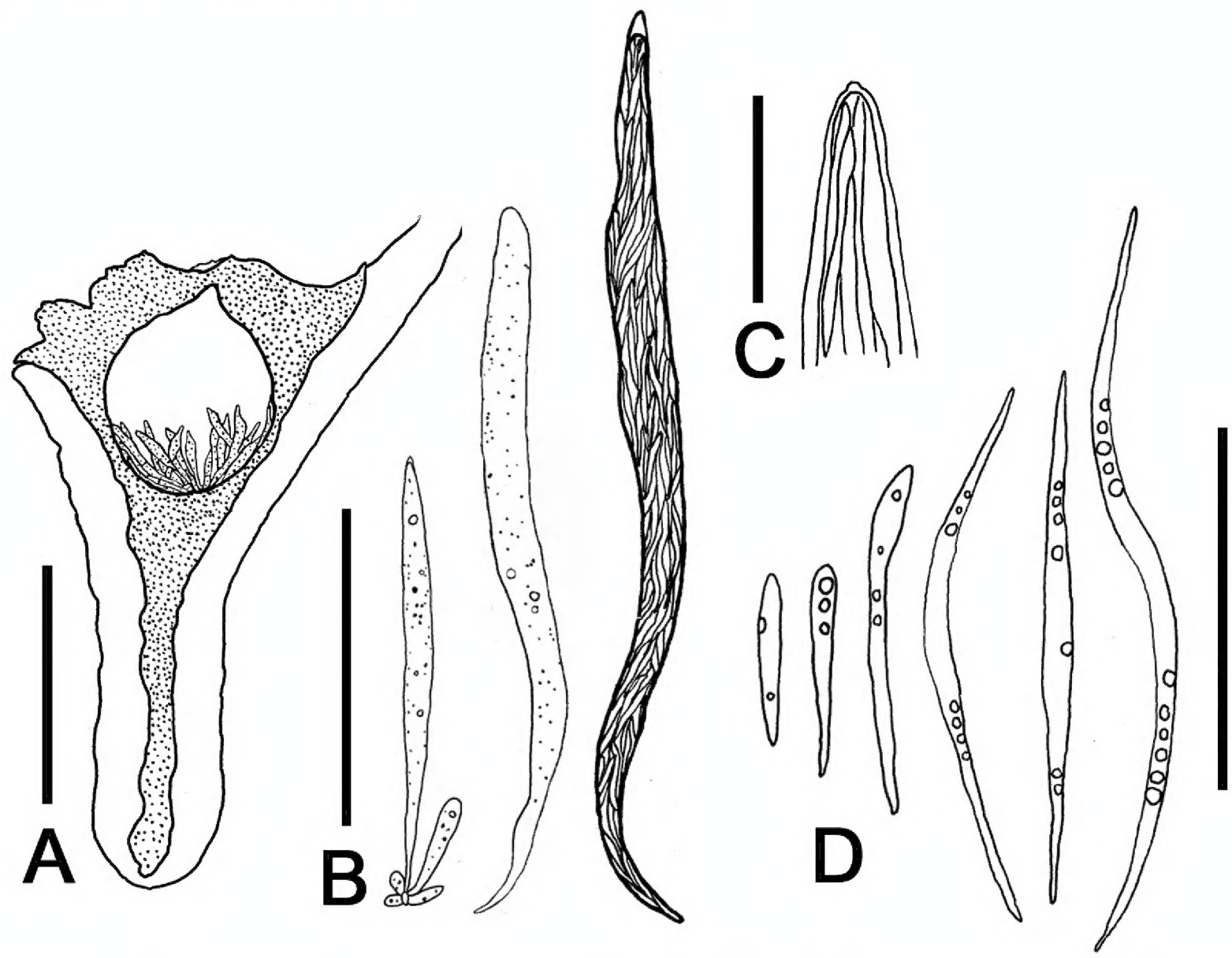

Figure 5. *Myriogenospora atramentosa*. **A.** Transverse section of a leaf blade of *Homolepis aturensis* with one perithecium (MP 528). **B.** Asci at different stages of development (MP 5114). **C.** Dome-shaped ascus tip (MP 4953). **D.** Two part-spore initials (on the left side) and four more or less mature part-spores after bipolar growth (MP 5114). Scale bars: A = 500 µm; B = 100 µm; C = 50 µm, D = 20 µm.

Known distribution. Until now, *Myriogenospora atramentosa* is known from Brazil, Colombia, Cuba, the Dominican Republic, Grenada, Nicaragua, Panama, Peru, Puerto Rico, Trinidad and Tobago, the United States, and Venezuela (Seaver and Chardon 1926; Viégas 1944; Hanlin and Tortolero 1990; Kirschner et al. 2010; Lenné 1990). The species has also been cited for Ghana, Nigeria, and Sierra Leone (Deighton 1936a; Lenné and Calderón 1989; Lenné 1990). Here, we report *M. atramentosa* for Costa Rica for the first time (Fig. 3B).

Known host plants. Until now, *Myriogenospora atramentosa* is known from *Andropogon bicornis* L., *A. gayanus* Kunth, *A. leucostachyus* Kunth, *A. virginicus* L., *Axonopus compressus* (Sw.) P. Beauv., *Brachiaria mutica* (Forssk.) Stapf, *Chloris gayana* Kunth, *Cymbopogon* sp., *Eragrostis hirsuta* (Michx.) Nees, *Eremochloa ophiuroides* (Munro) Hack., *Ichnanthus pallens* (Sw.) Munro ex Bent., *Imperata brasiliensis* Trin., *Panicum anceps* Michx., *P. hemitomon* Schult., *P. scoparium* Lam., *Paspalum ciliatifolium* Michx., *P. conjugatum* P.J. Bergius, *P. dilatatum* Poir., *P. laeve* Michx., *P. notatum* Flügge, *P. pilosum* Lam., *P. scrobiculatum* L., *P. urvillei* Steud., *Saccharum brevibarbe* (Michx.) Pers., *S. contortum* (Elliott) Nutt., *S. giganteum* (Walter) Pers., *S. officinarum* L., *Schizachryrium scoparium* (Michx.) Nash, *Sorghastrum nutans* (L.) Nash, *Sporobolus indicus* (L.) R.Br., and *Tridens flavus* (L.) Hitchc. (Seaver and Chardon 1926; Deighton 1936b; Viégas 1944; USDA Crops Research Division Agriculture Research Service 1960; Luttrell and Bacon 1977; Hanlin and Tortolero 1990; Lenné 1990). Here, we report *M. atramentosa* on *Homolepis aturensis* (Kunth) Chase for the first time.

Viégas (1944) cited *Microstachys speciosa* as host species of *M. atramentosa*. We assume that Viégas (1944) copied this information from Möller (1901) (see above) and erroneously considered *M. linearis* a synonym of *M. atramentosa*.

Phylogenetic analysis

We extracted DNA from *Myriogenospora* spp. (see specimen data above) and from specimens of additional species of Clavicipitaceae:

***Balansia discoidea* Henn.** Costa Rica • Limón Province, Puerto Viejo de Talamanca, between Coclé and Punta Uva, Finca One World; 09°37′31″ N, 082°42′56″ W; alt. approx. 46 m a.s.l.; 3 Jan. 2015; M. Piepenbring, C. Tiemann, O. Cáceres, M. Eichenlaub, M. Mardones leg.; on leaves of *Panicum pilosum* Sw. (det. M. Piepenbring); MP 5239b (M 141350).

***Balansia* sp.** Mexico • Yucatán Province, between Mérida and Chichen Izá, Libre Unión; alt. approx. 10 m a.s.l.; 21 Oct 1995; M. Piepenbring leg.; on leaves of *Bothriochloa pertusa* (L.) A. Camus (det. M. Piepenbring); MP 1934 (M 141352).

***Epichloë sylvatica* Leuchtm. & Schardl.** Germany • Hesse State, Kreis Groß-Gerau, Mörfelden-Walldorf, close to parking ground "Schützenhaus"; 49°58′16″ N, 008°32′33″ E; alt. approx. 150 m a.s.l.; 15 Jun. 2013; H. Lotz-Winter leg.; on leaves of *Brachypodium sylvaticum* (Huds.) P. Beauv. (det. H. Lotz-Winter); HLW 2038 (M 141353).

***Nigrocornus scleroticus* (Pat.) Ryley.** Benin • Atakora Department, Kossokouangou; 10°10′37″ N, 001°12′13″ E; alt. approx. 570 m a.s.l.; 17 Sep. 2015; L. Beenken, N. S. Yorou, M. Piatek, R. Mangelsdorff et al. leg.; on leaves of *Andropogon gayanus* Kunth (det. prelim. M. Piatek); LB 2015.09.17/1 (M 141359; UNIPAR). • Atakora Department, at road RN11 South of Kouandé; 10°15′37″ N, 001°39′15″ E; alt. approx. 490 m a.s.l.; 18 Sep. 2015; L. Beenken, N. S. Yorou, M. Piatek, R. Mangelsdorff et al. leg.; on leaves of *Andropogon schirensis* Hochst. (det. M. Piepenbring); LB 2015.09.18/1 (M 141360; UNIPAR). • Borgou Department, Wari Maro, South of Mont Soubakperou; 09°08′20″ N, 002°09′42″ E; alt. approx. 410 m a.s.l., 24 Jul. 2015; L. Beenken, N. S. Yorou, M. Piatek, R. Mangelsdorff et al. leg.; on leaves of *Andropogon gayanus* Kunth (det. prelim. M. Piatek); LB 2015.09.24/1 (M 141362; UNIPAR).

In total, we generated 24 sequences for six species of Clavicipitaceae including 21 sequences for five species of Balansieae. These sequences correspond to six ITS sequences, 12 nrLSU sequences, and six TEF1 sequences. Sequence alignments included 19 sequences/560 base pairs for ITS, 39/589 for LSU, and 23/999 for TEF1. The combined sequence data set includes 46 specimens of 33 species and had an aligned length of 2148 base pairs.

The Bayesian inference analysis and the ML analyses resulted in similar topologies; therefore, we present here only the ML tree for this dataset (Fig. 6). According to our results, the family Clavicipitaceae (100/1.00) as well as the tribes Balansieae (84/0.97) and Clavicipiteae (79/0.98) including the genera *Claviceps* (four species) and *Epichloë* (10 species) are monophyletic with significant statistical support. The genera *Claviceps* (94/1.00) and *Epichloë* (99/1.00) are also monophyletic. Within Balansieae, we found four monophyletic clades (A–D), three of them with significant statistical support. The *Myriogenospora* clade (A) (100/1.00) includes the species *M. atramentosa* (6 specimens). The *Nigrocornus* clade (B) (70/0.95) includes the species *B. nigricans* (1 specimen) and *N. scleroticus* (6 specimens). The first *Balansia* clade (C) (14/0.50) shows no significant support and includes the species *B. claviceps* (type species of *Balansia*), *B. cyperi, B. hypoxylon*, *B. texensis, Ephelis japonica*, *M. linearis*, and *Parepichloë cinerea*. The second *Balansia* clade (D) (75/0.97) includes the species *B. brunnans*, *B.* sp., *B. discoidea*, *B. epichloë*, *B. henningsiana*, *B. pilulaeformis*, and *B. strangulans*. We found no clustering of *M. linearis* and the type species of *Myriogenospora*, i.e., *M. atramentosa*. Instead, *M. linearis* is embedded in a clade comprising of mostly *Balansia* spp. Therefore, we refer to the specimen MP5242 from Costa Rica by the name *Balansia linearis* (*M. linearis*).

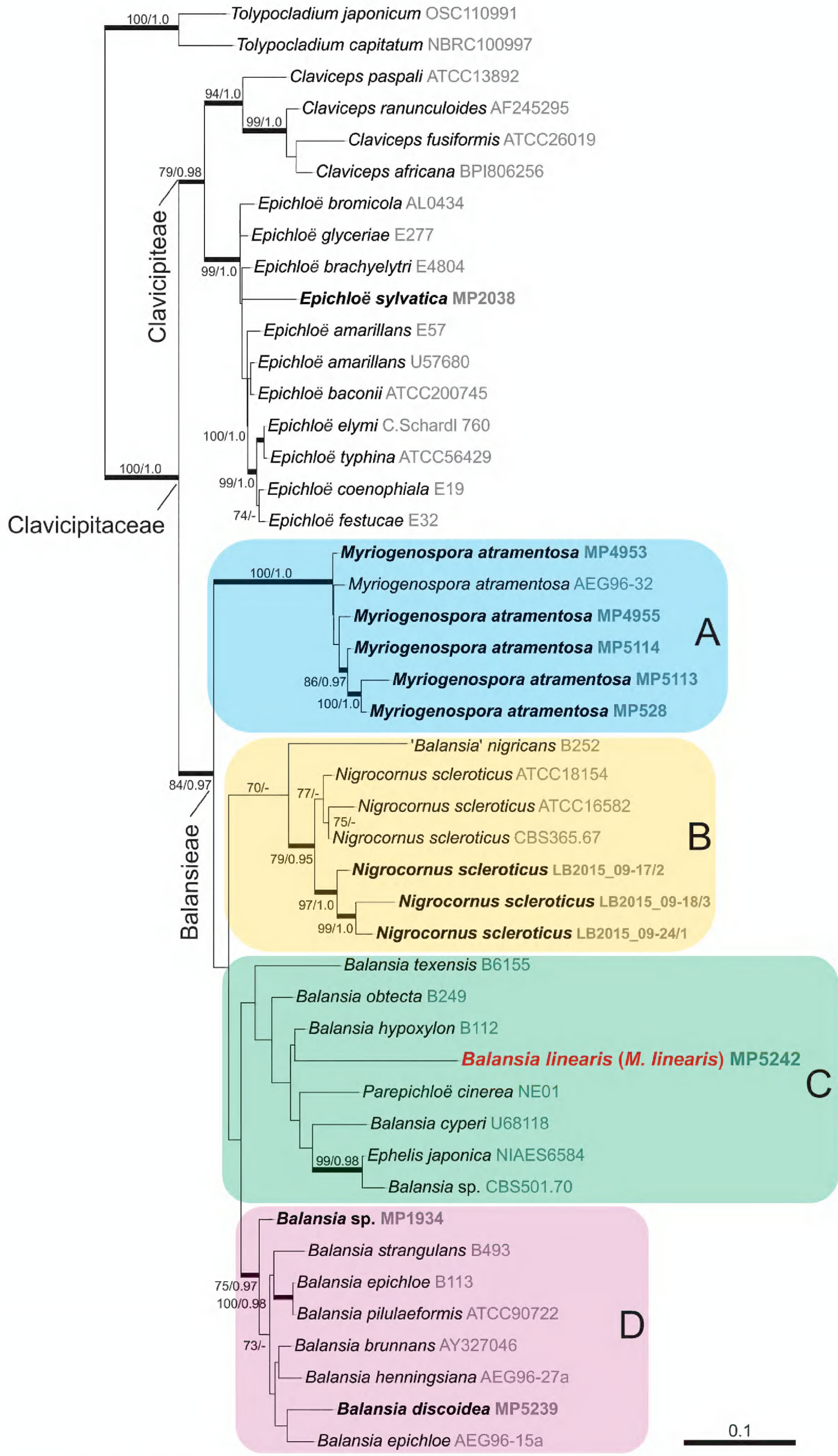

Figure 6. Phylogenetic relationships within the tribe Balansieae (Clavicipitaceae, Hypocreales, Ascomycota) focusing on *Myriogenospora* spp. This maximum likelihood (ML) phylogeny is based on three nuclear markers (nrLSU, ITS, TEF1). Support values are ML bootstrap values based on 1000 replicates and posterior probabilities from a Bayesian analysis. Values of ML BS >70% and Bayesian PP > 0.95 are given at nodes at the first and second positions, respectively. Internal branches considered strongly supported by both analyses are indicated by thickened branches.

Discussion

We propose to place *Myriogenospora linearis* in the genus *Balansia* as *B. linearis* (Rehm) Diehl due to (i) the contradictions of key morphological characteristics presented by White and Glenn (1994) with observations by us, Pazschke (1896), Möller (1901), and von Höhnel (1910), (ii) no support for a close relationship of *B. linearis* (*M. linearis*) with *M. atramentosa* (type species) in our phylogenetic analysis, and (iii) different host relationships.

(i) White and Glenn (1994) described *B. linearis* (*M. linearis*) part-spores as fusoid with a resemblance to *M. atramentosa* part-spores. However, our morphological analysis showed the presence of cylindrical part-spores with blunt tips for *B. linearis* (*M. linearis*). Earlier studies describe these part-spores as filiform (Pazschke 1896; von Höhnel 1910) or rod-shaped (Möller 1901). The distinct ascus morphologies further highlight the disparity of the two species as the ascus tips of *B. linearis* (*M. linearis*) are truncate and present light refractive bodies as in most clavicipitaceous and balansioid fungi (Jones and Clay 1987) whereas the dome-shaped tips of *M. atramentosa* are a unique, possibly derived feature of this species (Luttrell and Bacon 1977). We believe that these inaccuracies in the part-spore description might have been caused by a deteriorated state of the *B. linearis* (*M. linearis*) specimens examined by White and Glenn (1994) caused by the age of the material, as their most recent specimen was collected in 1934. Furthermore, the language barrier could be a source of errors as the relevant studies (Möller 1901; von Höhnel 1910) were published in German.

(ii) We found no evidence for a monophyletic clade that includes *Balansia linearis* (*M. linearis*) and *M. atramentosa*. Therefore, *B. linearis* is unlikely a member of *Myriogenospora* despite the similar linear stromata wrapped in leaf blades.

(iii) Host plants of *Balansia linearis* (*M. linearis*) are classified as members of the BOP clade whereas *M. atramentosa* hosts are classified in the PACMAD clade of Poaceae (Grass Phylogeny Working Group II 2012; Soreng et al. 2015). All fungi reported as *B. linearis* (*M. linearis*) infect species of the subfamily Bambusoideae, whereas *M. atramentosa* infects species of Chloroideae and Panicoideae. This difference in host range emphasizes the disparity between the *B. linearis* (*M. linearis*) and *M. atramentosa*.

By placing *B. linearis* (*M. linearis*) and *M. atramentosa* in distinct genera, we conclude that the presence of linear epibiotic stromata with regular files of perithecia surrounded by leaf blades and numerous part-spores in the asci are less indicative of systematic relationships than ascus tip structure and part-spore shape.

Our study on *Myriogenospora* spp. demonstrates that we require more information on Balansieae systematics to optimize our knowledge on the systematic position of balansioid fungi such as *B. linearis* (*M. linearis*). This study confirms that the tribe Balansieae, which includes the genera *Balansia*, *Ephelis*, *Myriogenospora*, *Nigrocornus*, and *Parepichloë*, is monophyletic but also highlights the need of a systematic revision of this taxon; we found at least three clades in Balansieae with significant support. All clades included *Balansia* species grouped with species from *Nigrocornus* and *Parepichloë*. These relationships confirm the paraphyly of the genus *Balansia* mentioned in previous studies (Kuldau et al. 1997; White et al. 2000). Some studies have created new monotypic balansioid genera based on morphological observations such as *Nigrocornus* and *Parepichloë* (White and Reddy 1998; Ryley 2003). Hence, an updated systematic revision could also lead to a classification of *B. linearis* (*M. linearis*) in its own separate genus as *Linearistroma lineare* (Rehm) Höhn. However, we recommend treating *L. lineare* as a member of *Balansia* until detailed morphological and complete molecular data of more species of Balansieae are available, especially those infecting BOP clade hosts such as *Balansia nigricans*, *B. texensis*, and *Heteroepichloë* spp. (Leuchtmann and Clay 1989; White et al. 1996; Tanaka et al. 2002).

Some of the species included in the phylogenetic analysis have broad geographical distributions spanning continents such as *B. claviceps* and *M. atramentosa*, which are reported from Old and New World habitats, or *N. scleroticus*, which is reported from Africa (i.e., Benin), Asia (i.e., India), and Australia. Misidentified specimens and the usage of species names for species complexes could cause these inaccuracies such as for *B. claviceps*, whose Asian specimens resemble descriptions of *B. andropogonis* Syd. (Leuchtmann 1993; Reddy et al. 1998). As *M. atramentosa* is reported from the Americas and Africa, specimens from these continents might belong to different species. Hence, sampling and generating sequence data from a range of populations could elucidate species identity, phylogenetic relationship, and geographical distribution of *M. atramentosa* specimens.

Future research should focus on fieldwork to obtain more fresh specimens of the generally rare and therefore poorly collected plant pathogenic species of Hypocreales (see Judith et al. 2015). These specimens will allow detailed morphological analyses and the generation of larger and more complete sequence data sets that will increase the statistical power of phylogenetic analyses for Balansieae. This approach combined with a host range analysis could resolve the systematics of this tribe and provide a systematically correct classification of *B. linearis* (*M. linearis*) amongst other balansioid fungi.

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Authors' Contributions

AC conducted detailed morphological and molecular analyses, contributed scientific drawings. AC and MM conducted phylogenetic analyses. MM compiled figures and tables and submitted sequences to GenBank. MP contributed most specimens, photos of fungi in the field, identified host plants, did preliminary identifications of the fungi, organized the infrastructure and permits. AC and MP wrote this article with input from MM.

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